

Does Phylogenetic Proximity Explain Nestedness in Mutualistic Ecosystems?

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ABSTRACT

We investigate how the pattern of contacts between species in mutualistic ecosystems is affected by the phylogenetic proximity between the species of each guild. We develop a dynamical model geared to establish the role of such proximity in the emergence of a nested pattern of contacts. We also define a parameter that provides a direct measure of the influence of phylogenetic proximity in a given pattern of contacts. We conclude that although phylogenetic proximity is compatible with nestedness it can not be claimed to be a cause of it. We find that nestedness can instead be attributed to a general rule by which species tend to hold contacts with counterparts that already have a large number of contacts. If the phylogenetic structure of both guilds is brought into the analysis, this rule is equivalent to maximize the phylogenetic diversity of the mutualistic counterparts of species of either guild.

keywords: Nested networks; Mutualistic communities; Phylogenetic proximity; Ultrametricity.

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I. INTRODUCTION

A sustainable management of ecosystems as well as a proper assessment of the impact of human activity on them can only be achieved with a proper understanding of the pattern of the interactions between the species. We are here interested in the case of mutualistic systems. These usually involve groups of animals and plants, helping each other to fulfill essential biological functions such as feeding or reproduction. This is the case of systems in which animals feed from fruits while dispersing the seeds (*seed dispersal networks*) or those where insects feed from the nectar of flowers while helping the plant in the pollination process (*pollination networks*).

The structure of such systems is described by means of an adjacency matrix whose elements represent the absence or presence of an interaction between the plant and animal species. In mutualistic networks this matrix strongly indicates that the mutualist ecosystems are not a random collection of interacting species, but that they display instead, a high degree of internal organization. A pervading feature that has been observed is that the adjacency matrix has a nested pattern of interactions, in which both generalists (species holding many interactions) and specialists (holding few interactions) tend to interact with generalists whereas specialist-to-specialist

interactions are infrequent [1]. In other words, if species are ordered by decreasing number of contacts, then the contacts of a given species constitute a subset of the contacts of the preceding species in the list [2].

The nested structure of mutualistic networks has been attributed to a number of different causes and the controversy about the ultimate reasons that make this pattern so frequently observed still remains. It is fairly obvious that a detailed explanation of the interaction behavior of individual species can be of little help to understand such a generalized pattern that is found across ecological systems of very different sizes and types, and involving plants of different nature and animals that range from insects to birds.

In Ref.[1] it is claimed that such order may offer some advantage for the robustness of the whole system thus suggesting that systems that are currently observed are those that have survived less disturbed thanks to its nested structure. Other, more elaborated theories have been proposed. In Ref.[3] nestedness has been attributed to phenotypic affinity between species of different guilds while in Refs.[4], [5] an extensive analysis is made concluding that phylogenetic proximity could explain the nested organization of contacts of some cases of mutualistic systems. In Ref. [6], on the contrary, the modest percentage correlations found between phylogenetic relatedness and ecological similarity, are taken to mean that phylogenetic relationships do not have a marked effect.

It has been customary to consider that the occurrence of some positive statistical correlation is a sign of causation for the occurrence of the nested pattern of contacts. However, the sole fact that in a part of the empirical observations two elements appear to be statistically cor-

related should not be taken to mean that one is the cause of the other. Such correlation may rather indicate instead that both elements are not incompatible, i.e., that they do not mutually exclude each other or that they stem from a third, common cause.

One example of this analysis is given by the strong positive correlation found between the species' abundance and hence the frequency of interactions, with the pattern of contacts of some species [7]. It has been suggested that locally abundant species are prone to accumulate interactions and conversely rare species are prone to lose them [8], as also suggested by neutral theories [9].

One alternative way to search for causal relationships is to explore the possible dynamic consequences of some assumed interaction mechanism, thus verifying or falsifying hypotheses concerning possible interaction mechanisms between the species. In Refs. [10], [11] we have proposed a Self Organizing Network Model (SNM), that allows to study the contact pattern of a system that is consistent with some hypothetical interaction mechanism between mutualistic species.

In the present paper we develop a modification of the SNM to take into account the effects of phylogenetic proximity in the build up of the contact pattern of the system. We also apply it to investigate the stability of such pattern of a real mutualistic system. The modified algorithm of the SNM includes the effects of phylogenetic proximity. Mathematically such proximity is accounted for through a matrix of distances separating any two species of each guild of the mutualistic system. The distance matrix is directly obtained from the topology of the phylogenetic tree. We aim in this way at establishing whether such proximity can be taken to be responsible for the emergence of a nested pattern of contacts.

II. METHODS: THE NUMERICAL MODELLING

A. The SNM

Mutualistic systems can be analyzed as bipartite graphs [12]. The interaction pattern is usually coded into a (rectangular) adjacency matrix in which rows and columns are labeled respectively by the plant and animal species. Its elements $K_{p,a} \in \{0, 1\}$ represent respectively the absence or presence of an interaction (contact) between the plant species p and the animal species a . The number of contacts of each species is the degree of the corresponding node in the bipartite graph.

Several reasons have been given to explain the pattern of interactions between the two guilds of a mutualistic network. They have been usually based on positive statistical significance of correlations. One way to elucidate a possible *causal* link between some hypothetical interaction mechanisms between mutualistic species and the pattern of contacts, is to use a dynamical model.

The basic idea behind this strategy is to verify the

consistency of the empirically observed contact pattern, and some hypothetical interaction rule that may favor or hamper the contact between mutualistic species. Such interaction can be assumed to be governed by, say, phenotypic complementarity, phylogenetic affinity, degree, or any other possibility. We refer to such interaction mechanism as a contact preference rule (CPR) in the sense that it is assumed that species that verify that rule tend to hold contacts among each other.

If a dynamical model is used having an assumed CPR as an ingredient, any lack of consistency between such CPR and the observed pattern of contacts will show up as instabilities of the results of the model. These may easily be detected when the observed adjacency matrix tends to be drastically altered if species are allowed to redefine their contacts to better fulfill some assumed CPR. On the other hand, the contact pattern and the assumed CPR can be seen to be consistent with each other if the contact pattern only suffers mild alterations when species redefine their contacts according to the CPR. The redefinition of contacts in accordance with some given CPR is accomplished with the SNM that we briefly explain below.

Within the same line of thought, it is also possible to check which is the contact pattern that would *emerge* from a random adjacency matrix if iterated changes according to a given CPR are allowed to take place. An emerging consistent contact pattern gives a clue of what one should expect to observe in nature if some given CPR is the prevailing interaction mechanism among the species of system.

From a purely theoretical point of view this set up is equivalent to consider that the observed pattern of interactions corresponds to an *optimal* assignment of the contacts between both guilds, with two constraints. The first constraint is the fulfillment of an assumed CPR, and the second, is the given (constant) total number of contacts between the two mutualist guilds. This number might be considered as an indicator of the energy invested by all the species of the ecological system in their exchange of nourishment. In other words one may attempt to describe the observed pattern of contacts as the result of a (combinatorial) *optimization* problem by which contacts in the adjacency matrix are placed in such a way as to reach an extreme of an utility function that corresponds to an optimal fulfillment of some prevailing CPR.

An example of a dynamical model incorporating some predefined CPR is the SNM developed in refs. [1],[10]. Within this model, the mutualistic system is assimilated to a bipartite graph and the topology of that network is established as the result of a self-organization process. This amounts to redefine links gradually and progressively alternating plants and animals. Say a plant is first chosen at random and one of its contacts is redefined by spotting a mutualistic counterpart with which it is possible a better fulfillment of the prevailing CPR. Next an animal is chosen and the same procedure is accomplished. An iteration of these steps provides a simple

heuristic, leading to a good approximation of the optimal assignment of contacts mentioned above.

Unlike in the preferential attachment algorithm [13], in the SNM the topology of a *non-growing* network with a fixed number of nodes is progressively reshaped: in each iteration a connection between two nodes of a different kind is rewired to favor a contact with the node having the highest degree. It is worthwhile noting that in this sense, the CPR of the SNM is *local*: it doesn't take into account the whole probability distribution, but only the degrees of the two randomly chosen species.

In the above references we show that that CPR always leads to nested networks with degree distributions that closely resemble the ones reported from the observation of real mutualistic systems.

It is worthwhile to point out that the self-organization process *does not pretend to represent a real life behavior* of plants and animals of the system. A starting random adjacency matrix is used as an initial condition for the dynamical process with the least possible bias. The whole process therefore does not aim at reproducing an evolutive or adaptive process. It rather provides a plausible mathematical tool to search for the pattern corresponding to an optimal assignment of contacts as explained above or to check for consistencies between some assumed CPR and the observed data.

The SNM that we have just described has to be modified to take into consideration the phylogenetic structure of both guilds. Therefore, it is necessary to have a simple quantitative measure of the phylogenetic structure of both guilds. We now describe how this is made.

B. The Ultrametric Organization of Phylogenetic Trees

The classification of species according to their similarities has been a major endeavor since the origins of biology as a natural science. The starting point of a classification of N species along this line is to have a symmetric $N \times N$ distance matrix with vanishing diagonal elements providing a measure of similarities and differences between any pair of species. Due to the central role of evolution, these classifications are depicted by phylogenetic trees that are determined using several sources of information.

Comparative studies of phenotypic traits are also widely used. The resemblance of species is measured through a phylogenetic signal that is quantitatively estimated through statistical analyses [14], [15] of the distribution of the values of different traits. These studies may also be supplemented whenever possible with fossil records.

While the tips of the tree correspond to presently observed species, the remaining nodes are associated to their presumed ancestors. A hierarchical organization of all living species is therefore provided and those that closely resemble each other are neighboring tips of the tree.

The phylogenetic classification of a group of species gather them in taxa within taxa of an ever increasing generality. This kind of arrangement gave place to pioneer taxonomic works using the concept of what now is known as ultrametric distance. In spite of the fact that ultrametricity had been used in biology since quite a long time (see, for instance, Ref.[16]), up to that moment this was a notion exclusively used by some mathematicians.

From a mathematical point of view, whenever this situation prevails the objects that are classified are said to be elements of an *ultrametric space*[17]. Based on the topology of the tree it is possible to define the *ultrametric distance* that provides a quantitative estimation of resemblances and differences between them. In the appendix we describe the simple procedure to extract a distance matrix directly from the topology of the phylogenetic tree.

An ultrametric distance matrix $d(k, k')$ constructed in this way is not only fully consistent from the start with the results of statistical analyses but also fully agrees with what can be expected from an intuitive picture: small values of $d(k, k')$ remain associated to species that share the same branching sequence and a common evolutionary history while large values correspond to species that have followed different evolutionary processes because they have been separated at earlier stages. With these conventions the closest possible distance between any two species is 1 and, if all species are at a distance 1 they belong to a *star phylogeny*.

C. The phylogenetic-SNM

We are now in the position to define the self organization process involved in the SNM using phylogenetic relatedness among the species of each guild.

The influence of phylogenetic proximity in the pattern of contacts can be cast into a modified SNM by properly defining a CPR based on the ultrametric distance between species of each guild.

In each step of this modified SNM a link of a randomly chosen species is also redefined. However this is made in such a way as to better fulfill a CPR by which phylogenetically close species - i.e. separated by a short ultrametric distance - tend to have the same contacts. The basic idea is to check either if this CPR gives rise to a nested pattern of contacts in the adjacency matrix when starting from a random initial condition or, if an initially nested pattern is stable under a dynamics induced by that CPR.

For each time-step of the algorithm, the following actions are performed:

- Two elements $K_{p,a_1} = 1$ and $K_{p,a_0} = 0$ are chosen at random in the same row p , corresponding to connected and disconnected species respectively.
- Two total ultrametric distances S_0 and S_1 are calculated between the plant p and the other plants p' which hold a contact with a_0 and a_1 respectively.

$$S_0 = \sum_{p'} d(p, p') K_{p', a_0} \quad (1)$$

$$S_1 = \sum_{p'} d(p, p') K_{p', a_1} \quad (2)$$

Notice that S_0 and S_1 are the total ultrametric distances separating the randomly chosen plant from all other plants holding contacts with the same animal. S_1 corresponds to the current contact and S_0 is calculated for an alternative location of the contact.

- A swap between this two elements corresponding to the redefinition of the link, i.e., $K_{p, a_0}^{\text{new}} \rightarrow 1$ and $K_{p, a_1}^{\text{new}} \rightarrow 0$, is proposed and it will be accepted if the following two conditions are satisfied:

- (i) neither animal species a_1 nor a_0 become extinct due to the swapping,
- (ii) $S_1 \geq S_0$

In this case a_0 is a better mutualistic counterpart of p ; it belongs to a group whose members are closer phylogenetic relatives than the original group of contacts of a_1 . Whenever the conditions (i) or (ii) are not met, the proposed swapping is rejected.

These steps are repeated, alternatively inverting the role of rows and columns, until the algorithm converges (no more changes are possible).

The CPR just described, which we call MIN-CPR, is certainly not the unique way to take into account the phylogenetic distance. It is interesting to consider the opposite rule, which we call MAX-CPR and which consists in replacing the condition (ii) by $S_1 \leq S_0$ to accept the swapping.

Since the MIN-CPR and MAX-CPR conditions are mutually exclusive we run two independent SNM algorithms.

Within the MIN-CPR possibility, the animal counterpart that will finally be selected for the plant p , is such that the set of plants p' having contact with the animal a_0 are phylogenetically closer to p than those in contact with a_1 . This is so because the sums S_0 and S_1 involve all distances between the plant p (that has been selected at random) and all other plants that hold contacts with the two animals a_0 and a_1 . With this algorithm the configuration of contacts is progressively dominated by phylogenetic proximity as measured by the corresponding distance matrices. Within this strategy species of one guild are assumed to interact in the same fashion as all other species of the same guild belonging to their phylogenetic neighborhood.

Within the MAX-CPR possibility, the animal counterpart that will be selected for the plant p is such that all

other plants p' that have some contact with it are phylogenetically further from p . In this way the set of species that share contacts with p tend to have a greater phylogenetic diversity. This is so because the pattern of contacts is progressively dominated by greater phylogenetic distances as measured by the corresponding distance matrices. In this alternative all species tend to be as generalist as possible in what refers their phylogenetic grouping.

In order to check the ordering process generated by the SNM we define an *effective distance between interacting species* as:

$$D^{A,P} = \frac{1}{\langle d_{A,P} \rangle} \frac{\sum_{k,k'} d_{A,P}(k, k') \tilde{W}_{k,k'}^{A,P}}{\sum_{k,k'} \tilde{W}_{k,k'}^{A,P}} \quad (3)$$

In Eq.(3) A and P respectively represent animals and plants, and \tilde{W} represents the unweighted adjacency matrix of the projected graphs for animals or plants that are defined as (with K^T being the transposed of K)

$$W_{p,p'}^P = \sum_a K_{p,a} K_{a,p'}^T (1 - \delta_{p,p'}) \quad (4)$$

$$W_{a,a'}^A = \sum_p K_{a,p}^T K_{p,a'} (1 - \delta_{a,a'}) \quad (5)$$

and $\tilde{W}_{k,k'} = 1$ if $W(k, k') \neq 0$ or 0 if $W(k, k') = 0$, i.e., two species share or do not share mutualistic counterparts; $d(k, k')$ stands for the same ultrametric distance matrix that has been used in the self organization algorithm. This equation provides different results for plants or animals and should therefore be evaluated separately for the two guilds.

The sum in the denominator of Eq.(3) is just the number of terms appearing in the numerator, therefore D represents the average distance between species of the same guild that share at least one counterpart of the other guild. D is measured in units of the average distance $\langle d \rangle$ between *all* plant (animal) species of the system, namely

$$\langle d_{A,P} \rangle = \frac{\sum_{k,k'} d_{A,P}(k, k')}{N_{A,P}(N_{A,P} - 1)} \quad (6)$$

where $N_{A,P}$ is the number of animal or plant species of the system.

A value $D^{A,P}$ significantly less than unity indicates that phylogenetic proximity is a dominant effect, because species that share at least one mutualistic counterpart are closer than the average separation of species of that guild. If species are ordered as the tips of a phylogenetic tree, $\tilde{W}_{k,k'}$ has most of its non vanishing elements close to the diagonal. If $D^{A,P} \geq 1$ or $D^{A,P} \simeq 1$ is instead a signature that phylogenetic proximity is not relevant. Correspondingly $\tilde{W}_{k,k'}$ tends to display non vanishing elements far from the diagonal. The value of $D^{A,P}$ is therefore a good order parameter characterizing the whole pattern of contacts and can also be used to check if the the ordering process implied in the SNM converges to stable configuration.

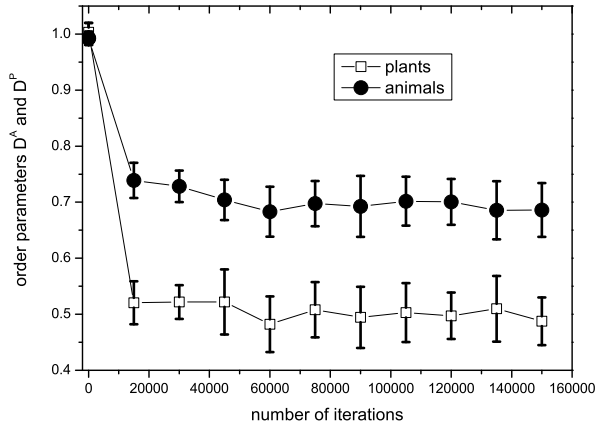


FIG. 1: Order parameters D^A and D^P (effective distance between species sharing the same mutualistic counterparts), as a function of the number of iteration steps of the SNM algorithm, using the MIN-CPR alternative. The curves are the average over several realizations with random initial conditions, always using the same number of rows, columns, and contacts than the system NCOR. Error bars are the corresponding standard deviations.

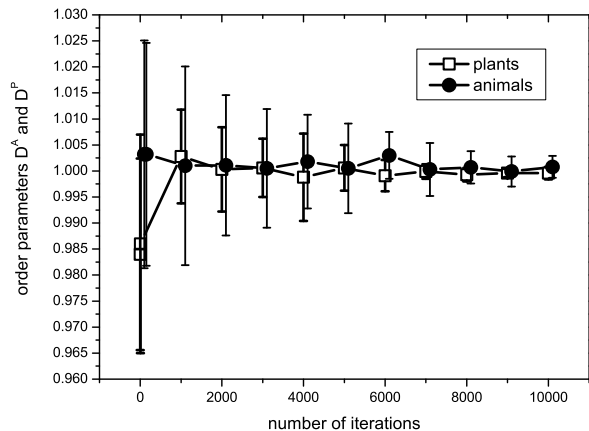


FIG. 2: Value of the order parameters D^A and D^P as a function of the number of iteration steps of the SNM algorithm using the MAX-CPR alternative. Notice that the vertical scale is strongly expanded as compared to that of Fig.1. Conventions are the same as in that figure. Data for plants and animals have been slightly horizontally displaced, to facilitate its observation.

III. RESULTS

We will concentrate our discussion on the case of the ecosystem Nava de las Correhuelas (NCOR) as reported in Ref. [4]. This system has been presented as an example where phylogenetic proximity explains the contact

pattern between mutualistic guilds and is therefore a very good case of study.

In Figs.1 and 2 we plot the values of the parameters D^A and D^P as a function of the number of iteration steps of the SNM for animals and plants for the two possible CPR's considered above.

The initial conditions are always adjacency matrices of the same number of rows and columns and with the same number of contacts than the observed NCOR system, except for the fact that all contacts are randomly distributed. The curves are the average over a statistically significant number of realizations of such random initial conditions. The error bars are the standard deviation of the results obtained over such set. These error bars provide also a measure of the convergence of the SNM.

As the number of SNM iterations grows both CPR's produce values of D^A and D^P that reach asymptotic constant values. This indicates that both CPR's succeed in driving the system to a stable and ordered pattern of contacts. These are however different. While for the MIN-CPR case it is found that the asymptotic value of the order parameters D^A and D^P stabilizes at values that are significantly smaller than unity, for the MAX-CPR alternative it is found instead that they reach a stable value of 1.

A value $D^A \simeq D^P \simeq 1$ indicates that the distance between species of the same guild that share the same mutualistic counterparts is close to the average distance of the corresponding guild, as determined by their respective phylogenetic trees.

As expected, this is the case for the first iterations, shown in both Figs.1 and 2. The system is very near the initial condition, where the contacts have been randomly distributed with no relation whatsoever to the phylogenetic tree of either guild.

It is interesting to compare such value with the one obtained by using the observed pattern of contacts of the NCOR system. The values obtained are $D^A \simeq D^P \simeq 0.98$ that are indistinguishable from those obtained for random adjacency matrices.

On the other hand, values significantly lower than 1 as those seen in Fig. 1 after many iterations of the SNM, indicate that species that share the same counterparts are close phylogenetic neighbors.

The ordered pattern that prevails asymptotically for the MAX-CPR case is a single, perfectly nested pattern [1]. After some initial fluctuations $D^{A,P}$ stabilize very closely to 1. The ordered pattern turns out to be essentially unique except for a random permutation of phylogenetic labels and therefore the error bars tend to diminish as the number of iterations of the SNM increases.

This is not the case for the MIN-CPR in which error bars do not diminish in the same way. The reason is that there are several possible distinct asymptotically ordered patterns, all of them corresponding to modular ecosystems and all having slightly different values of D^A and D^P . The phylogenetic SNM is seen to converge to any of

these ordered patterns thus producing a somewhat larger dispersion in the values of these parameters. In all cases however, the limiting constant values that are reached greatly differ from 1 that is many standard deviations away.

The SNM algorithm can also be used to test if some given pattern of contacts is compatible with a CPR involving some kind of phylogenetic dependence. This can be made through the study of its *stability*. The asymptotic contact pattern can give a clue of what kind of pattern one should expect to find for each prevailing CPR. In Fig.3 we show the adjacency matrix of the SNM system as obtained after a great number of iterations (panels (B) and (C)). These are the asymptotic contact patterns obtained when applying the MIN-CPR and the MAX-CPR respectively. Since we are performing a stability analysis we have always used as initial conditions the empirically observed contact pattern that is shown in Panel (A). These matrices correspond to configurations in which the parameters $D^{A,P}$ have reached an almost stationary value and are therefore nearly optimal in the sense explained in the preceding section. In the same figure are shown the phylogenetic trees taken from Ref. [4] of plants and animals to guide the eye. While in panels (A), (B) and (C) the rows and columns of the adjacency matrix have been ordered as in the tips of the corresponding phylogenetic trees, in panel (D) the species of both guilds have been instead ordered according to their degree with the purpose of rendering more evident the nested pattern of contacts.

The MIN-CPR corresponds to a rule in which the search of contacts is dominated by phylogenetic proximity. To better understand the emerging contact pattern shown in Panel (B), one has to bear in mind that both animals and plants are considered on equal footing. This gives rise to an adjacency matrix that breaks into disconnected blocks in which phylogenetically close species of one guild interact with a similar group of the other guild. This is the opposite of a nested scheme since the species tend to specialize its contacts. By the same token, generalists are ruled out of the system. The contact pattern of the NCOR system used as an initial condition, becomes therefore severely disturbed putting in evidence that it is unstable under the presence of the MIN-CPR in which phylogenetic proximity is the dominant rule.

A similar analysis for the MAX-CPR situation shows an opposite behavior. The SNM causes no drastic reorderings, reinforcing instead the presence of generalists and keeping the matrix mildly changed (see panel C). The observed adjacency matrix must therefore be considered stable under such CPR. This run of the SNM also provides additional information. The NCOR system hosts a group of animals that are phylogenetically close and that are all fairly good generalists (e.g. the *turdus* group). Such correlation between degree and phylogenetic proximity is not destroyed by the perturbations introduced

by the SNM, if the prevailing CPR is of the MAX type (compare panels (A) and (C)).

An additional effect of the iteration of the MAX-CPR rule is that it leads to an asymptotically stable contact pattern that is almost perfectly nested. As mentioned before, in panel (D) we show the adjacency matrices of panels (A) and (C) in which species have been reordered according to increasing degree; in this way we can compare the empirically observed nested structure of the NCOR system with an asymptotically nearly perfect nested pattern produced by the SNM using the MAX-CPR. Since the observed NCOR system is considerably nested, the effects of the SNM are not drastic.

The occurrence of phylogenetically close species with similar degrees and the occurrence of a nested pattern should therefore be considered as independent from each other. When speaking of a *cause* for nestedness one should expect an element that is present in *all* the observed systems, with perhaps minor variations in few individual cases. We have found here that the MAX-CPR strategy always converges to a nested pattern.

However this alternative combines phylogenetic effects with those just mentioned due to the number of contacts. This is because contacts are relocated according to a larger sum S_1 or S_0 ; and this occurs not only by involving species that are more phylogenetically distant but also by involving a *greater number* of counterparts as reported in [10]. In order to separate both effects we have made an alternative test dividing both sums by the number of counterparts that are found in both rows. In this way contacts are placed in those positions that correspond to a greater *average* phylogenetic distance. This test completely separates phylogenetic influence from any other. The results of these calculations point in the direction that a stationary stable contact pattern is never reached thus confirming what was said in Ref.[10] namely that the chief effect leading to a nested configuration is that all species tend to place their contacts with already crowded counterparts. Since on the other hand nestedness is not destroyed by the self organization process, phylogenetic proximity has therefore to be considered *compatible* with a rule inducing nestedness but is far from being a cause of it.

The above arguments have a greater reach because they hold for *any* distance matrix or similarity measure. We have made a separate test by checking the stationary contact patterns that are obtained by introducing alternative phylogenetic trees. We have considered trees that display a uniform branching rate and another in which all species successively stem from a single branch. Notice that in the case of a star phylogeny the self organization algorithm becomes identical to that of Ref.[10]. We have found that in all cases the MIN-CPR strategy leads to modular ecosystems in which contacts gather in nearly disconnected groups. As long as it is imposed that contacts have to take place between species that are close to each other, according to some criterion, some kind of specialization is favored and nestedness turns out to be

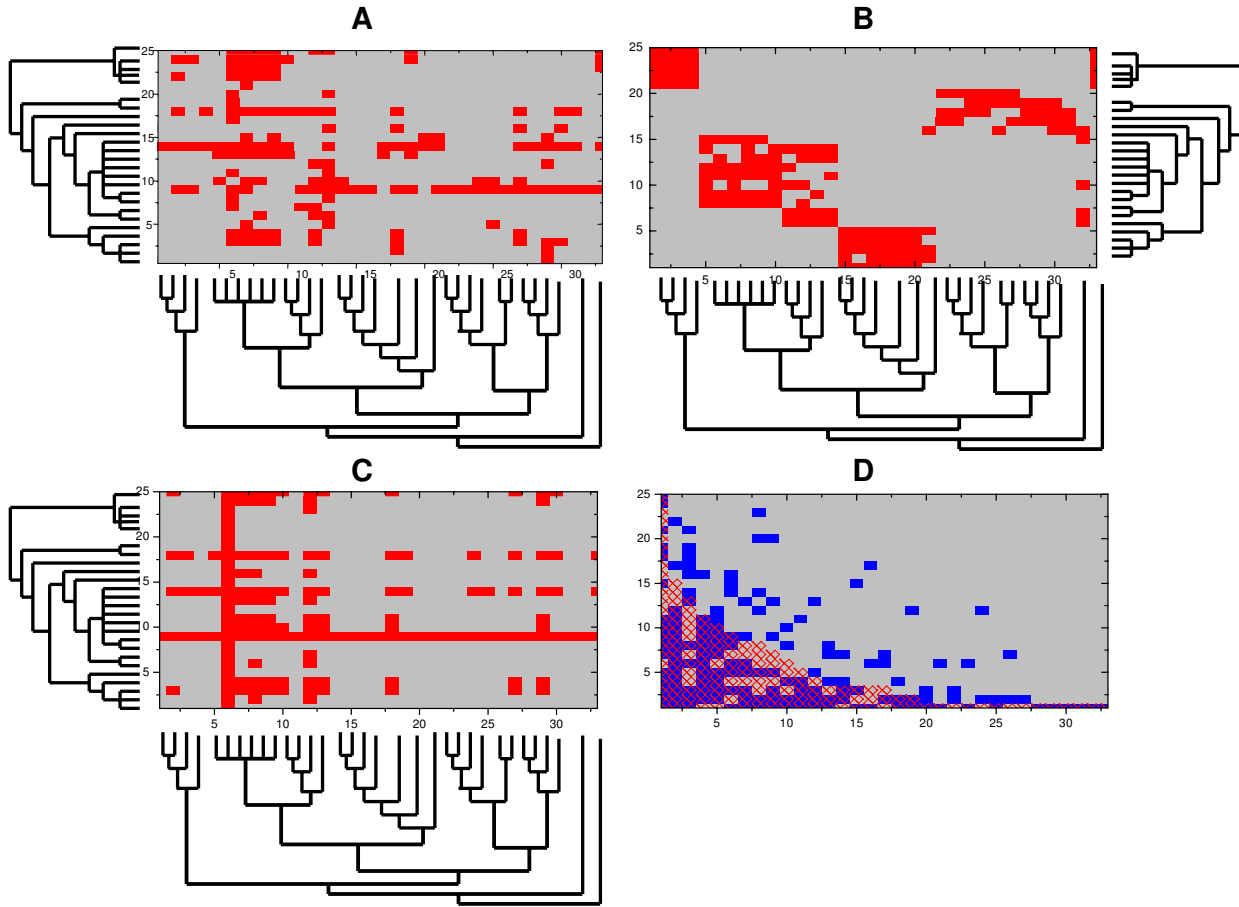


FIG. 3: Several adjacency matrices for the study of the NCOR ecosystem. Panel(A): the empirical contact pattern with species ordered according to the phylogenetic tree (shown along both margins of the matrix); panel(B): contact pattern produced by the SNM after 80,000 iterations using as input the empirical matrix shown in panel (A) and the MIN-CPR alternative, species in the same order as in panel (A); panel (C): contact pattern produced by the SNM after 5000 iterations, using MAX-CPR, species in the same order as in panel (A); panel (D) same contact pattern as panel (A) (dark pixels) and (C) (hatched pixels) but species are ordered by their degree. Dark pixels correspond to observed contacts (panel (A)) while slanted pattern corresponds to the theoretical results (panel (C)). Notice that while in panel (C) there are generalists and specialists, they don't show up in panel (B).

hampered and not favored. The opposite is also true: whenever contacts take place with a greater variety of counterparts, nestedness can be expected to occur.

IV. CONCLUSIONS

The general conclusion that stems from the SNM is that an interaction between species that exclusively prefers phylogenetic proximity can never give rise to a nested contact pattern. Nestedness turns out to be unstable in the presence of such interaction rule. This can be seen by noting that such interaction mechanism relies in the generalized occurrence of species that are special-

ists and ruling out generalists that are an indispensable ingredient of a nested organization. A CPR governed by phylogenetic proximity for *both mutualists guilds* tends to destroy a nested pattern of contacts giving rise to adjacency matrices with a clear tendency to break down into separate, nearly independent components in which groups of phylogenetically close neighbors of both guilds hold contacts among each other but not with the rest of the species of the ecological system.

We have also shown that an alternative interaction pattern dominated by *phylogenetic diversity* is instead a much better approach to describe real situations. This interaction mechanism is one in which species hold contacts with the greatest possible diversity of mutualist counter-

parts that are already visited by a greater number of species. This rule is fully consistent with the ones tested in Refs.[10], [1]. Highly realistic degree distribution functions and contact patterns are produced by the SNM with only that assumption.

If a group of phylogenetically close species happen to have similar contact patterns, this turns out to be stable under such maximal diversity interaction rule. In fact, a set of phylogenetically close species that also are fairly good generalists remains stable under the organization algorithm of the SNM. We thus found, in agreement with Ref.[18], that phylogenetic affinity is *compatible* with a nested pattern of contacts, therefore explaining statistically significant correlations between degree distributions and phylogenetic proximity. However the results of the SNM place serious doubts to consider that such correlations are a sign of causation. The few circumstances in which they have been found to be statistically significant [4], [6], point into the direction of considering that these are largely accidental.

We have also tested the present model in other mutualistic systems; the results are identical to those of the NCOR system and therefore we omit them here. A dominant cause of the generalized nestedness found in mutualistic ecosystems perhaps lies on the simple fact that species that we observe in real systems today are those that tend to put the least possible restrictions on their mutualist counterparts.

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Appendix: the ultrametric distance matrix

If a tree-like diagram is provided it is also possible to extract from it a square matrix $d(k, k')$ of all ultrametric distances between any two living species k and k' . One biologically plausible way to define such distance is to extract it from their evolutionary history. This amounts to consider that two species are “separated by a distance” that is measured by the time elapsed since they were differentiated in the course of evolution. This distance satisfies a modified triangular inequality: for any three species k, k' and k'' , $d(k, k'') \leq \text{Max}\{d(k, k'); d(k', k'')\}$ that should be compared to the *metric* triangular inequality $d(k, k'') \leq (d(k, k') + d(k', k''))$

The evolutionary time can be represented by the length of the branches of the tree. The ultrametric distance between any two species k and k' is therefore given by the total length of the branches that have to be climbed starting either from k or k' until a common ancestor is found. It is of course clear that since the tree-like diagram is compatible with the analysis of the phylogenetic signal, the ultrametric distance extracted from the same phylogenetic tree is also compatible with those stemming from statistical analyses. Resemblances and differences measured by this ultrametric distance could be considered to involve a compound effect of all the traits that were considered in the analyses that lead to the phylogenetic tree.

To obtain the ultrametric distance, a length should be ascribed to the branches of the phylogenetic tree. Since the true lengths of these segments are in general unknown some model assumption has to be made. In comparative studies there is not a universally accepted criterion [15] concerning this point and in many analyses all the lengths of the branch segments are set equal to a constant value since this may be considered to make fewer assumptions about the data.

In order to get a square matrix with all the ultrametric distances one has to provide a uniform time scale for all branches, i.e., to provide a time order for all the branching points of the phylogenetic tree. The most parsimonious way of doing this is by defining that all branches that stem from a common ancestor and reach the tips of the tree must have the same length, counting lengths by starting from the tips and climbing upwards. This assumption is consistent with the constancy of an evolutionary clock [16].

With this procedure the distance matrix can directly be read from the topology of the phylogenetic tree. We exemplify this procedure in Fig.4. We define that the two branches that lead to the species labelled (4) and (5) having a common ancestor in node (A) have a length equal to 1. By the same rule, the branch starting at species (3) that has a common ancestor with (4) and (5) in the branchpoint (B) has a length equal to 2. Moreover, the total length of the branches that have to be climbed starting from (1) or (2) to reach a common ancestor to all species in (C) must then have a total length of 3. In all these cases the lengths are defined except for an overall multiplicative scale factor. This ambiguity is however not relevant for the present analysis.

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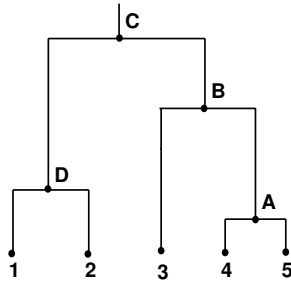


FIG. 4: An example of a simple phylogenetic tree is shown. The matrix of ultrametric distances is: $d(1, 2) = d(4, 5) = 1$ $d(1, 3) = d(1, 4) = d(1, 5) = d(2, 3) = d(2, 4) = d(2, 5) = 3$ $d(3, 4) = d(3, 5) = 2$

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